

## THE GENERA OF ZYGOPHYLLACEAE IN THE SOUTHEASTERN UNITED STATES <sup>1</sup>

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ZYGOPHYLLACEAE R. Brown in Flinders, *Voy. Terra Austral.* 2: 545. 1814,  
"Zygophylleae"

(BEAN-CAPER FAMILY)

Annual to perennial [often suffrutescent] herbs [shrubs] or occasionally trees; branches usually divaricate, with angled or swollen nodes, growth sympodial. Leaves opposite [occasionally alternate], even-pinnately compound, [sometimes odd pinnate, occasionally simple or 2-foliolate, rarely 3–7-foliolate], often fleshy to coriaceous, persistent, petiolate [to subsessile]; leaflets entire [sometimes lobed], inequilateral, petiolulate to subsessile; stipules paired, free, foliaceous [sometimes fleshy or spinescent], persistent or rarely deciduous to caducous. Flowers [4] 5 [6]-merous, perfect, hypogynous, regular or occasionally slightly irregular; peduncles terminal or pseudaxillary, 1-flowered, solitary or occasionally few to many. Sepals [4] 5 [6], free or rarely slightly connate basally, imbricate in bud, persistent or occasionally deciduous. Petals as many as sepals, free [rarely connate basally], often clawed, sometimes twisted, imbricate or convolute, deciduous, rarely marcescent. Extrastaminal and/or intrastaminal glandular disc usually present and conspicuous. Stamens in [1] 2 [or 3] whorls of 5 each, outer[most] whorl usually opposite petals, often alternately unequal in length or sterile; filaments free, subulate to filiform [rarely winged], frequently glandular [or appendaged] basally, outer whorl occasionally adnate basally to petals, inserted on or below disc; anthers 2-loculate, subbasifixed to versatile, introrse, longitudinally dehiscent. Gynoecium [2–] 5-carpellate, syncarpous; style terminal, usually simple;

<sup>1</sup> This treatment was prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator, C. E. Wood, Jr.). The format is that established in the first paper in the series (*Jour. Arnold Arb.* 39: 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional material from extraterritorial taxa in brackets. References that I have not seen are marked by an asterisk.

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stigma minutely and obscurely lobed to distinctly ridged; ovary superior, [2-]5-10[-12]-lobed and -loculate, sessile or rarely on a short gynophore; ovules 1 or 2 to many in each locule, pendulous [or ascending], anatropous, placentation axile [rarely basal]. Fruit a [2-]5-lobed septicidal [or loculicidal] capsule or a schizocarp splitting lengthwise into 5-10[-12] hard, tuberculate to spiny [or winged] mericarps [rarely a drupe or berry]. Seeds 1 to several [to many] in each locule, endosperm present or absent; embryo with flat cotyledons. TYPE GENUS: *Zygophyllum* L.

Twenty-six genera and about 250 species, widely distributed, but mainly in the warmer, drier regions of the world. Eight genera are represented in North America: *Guaiaacum* L., with one native and several cultivated species in southern Florida; *Kallstroemia* Scop., with six native and one introduced species, mainly in the Southwest; *Peganum* L., with *P. mexicanum* Gray native to Texas and *P. harmala* L. introduced into the Southwest from the Old World deserts; *Larrea* Cav., with *L. tridentata* (DC.) Coville widely distributed in the deserts of the southwestern United States; *Porlieria* Ruiz & Pavón, with *P. angustifolia* (Engelm.) Gray in Texas; *Tribulus* L., with two introduced species; and *Zygophyllum* L., with the introduced *Z. Fabago* L. Species of *Guaiaacum*, *Kallstroemia*, and *Tribulus* occur in our area.

The Zygophyllaceae are a somewhat isolated family with no close relatives, except perhaps for the Balanitaceae. The family has recently been placed in the Geraniales (Takhtajan, 1959, 1969; Scholz, 1964; Thorne, 1968), Malpighiales (Hutchinson, 1959, 1969, in his Lignosae), and Sapindales (Cronquist, 1968). Airy Shaw (1966) thinks that they are closely related to the Rutaceae; Hutchinson (1969) supposes that they are derived from the Linaceae; and many authors place them near the Erythroxylaceae, Geraniaceae, Oxalidaceae, and other Geraniales *sensu* Engler, but these taxa do not appear to be closely related. The best indication of the families to which they are allied is that of Cronquist (1968), who places them with his Sapindales-Geraniales-Linales-Polygalales complex.

The latest subfamilial classification of the family (Scholz, 1964), follows that originally published by Engler (1890, 1896); It is still a far from satisfactory treatment. The Zygophyllaceae at present are divided into seven subfamilies: Augeoideae Engler (*Augea* Thunb.), Chitonioideae Engler (*Morkillia* Rose & Painter, *Viscainoa* Greene), Nitrarioideae Engler (*Nitraria* L.), Peganoideae Engler (*Malacocarpus* Fischer & Meyer, *Peganum*), Tetradiclidoideae Engler (*Tetradiclis* Stev. ex Bieb.), Tribuloideae D. M. Porter (*Kallstroemia*, *Kelleronia* Schinz, *Tribulopsis* R. Br., *Tribulus*),<sup>2</sup> and Zygophylloideae (*Bulnesia* C. Gay, *Fagonia* L., *Guaiaacum*, *Larrea*, *Metharme* Phil. ex Engler, *Miltianthus* Bunge, *Neolue-*

<sup>2</sup> These four genera, which form a natural group within the family, have been discussed in detail elsewhere (Porter, 1969a, pp. 42-46). They deserve recognition as subfamily **Tribuloideae** D. M. Porter, stat. nov. (Based on tribe Tribuleae H. G. L. Reichenbach, *Conspectus Regni Veg.* 199. 1828.)



*deritzia* Schinz, *Pintoa* C. Gay, *Plectrocarpa* Gill., *Porlieria*, *Seetzenia* R. Br., *Sericodes* Gray, *Sisyndite* E. Meyer ex Sonder in Harvey & Sonder, *Tetraena* Maxim., and *Zygophyllum*). All but the last appear to be natural taxa, and further study undoubtedly will result in a rearrangement of the Zygophylloideae. Hutchinson (1967) has provided an excellent key to the genera of the family.

Palynological studies (Erdtman, 1952; Agababian, 1964; and Kaligis-Walalangi, 1969) indicate a heterogeneity of pollen types within the family, especially within the Zygophylloideae as recognized above. A combination of data from palynology, comparative anatomy and morphology, and cytology should provide a more rational treatment of this subfamily. Pollen morphology and wood anatomy support the removal of *Balanites* Del. and the recognition of the family Balanitaceae, intermediate between Zygophyllaceae and Simaroubaceae.

Reported chromosome numbers are *Bulnesia Retamo* (Gill.) Griseb. ex Hooker,  $2n = 26$  ( $x = 13$ ); *Fagonia* (6 spp.),  $2n = 18, 20, 22$ , ca. 24 ( $x = 9$ ); *Guaiacum officinale* L.,  $2n =$  ca. 26; *Kallstroemia pubescens* (G. Don) Dandy in Keay,  $2n = 32$ ; *Larrea* (5 spp.),  $2n = 26$ , ca. 26, 52, ca. 52 ( $x = 13$ ); *Malacocarpus crithmifolius* (Retz.) C. A. Meyer,  $2n = 24$ ; *Nitraria* (3 spp.),  $2n = 18, 24, 48$ , ca. 48, 60 ( $x = 12$ ); *Peganum Harmala*,  $2n = 22, 24$ ; *Tribulus* (2 spp.),  $2n = 12, 24, 36, 48$  ( $x = 6, 12$ ); *Viscainoa geniculata* var. *pinnata* I. M. Johnston,  $2n = 26$ ; *Zygophyllum* (18 spp.),  $2n = 16, 18, 20$ , ca. 20, 22, 44 ( $x = 8$ ).

Many studies have been made of the wood anatomy of various taxa in the family. The wood is highly specialized, and the species studied form a distinctive, natural group. The specialized features (cf. Metcalfe & Chalk, 1951, p. 291) are "a vessel member length of 0.1–0.2 mm., storied structure, homogeneous rays and fusiform parenchyma cells, with several other features, such as solitary vessels, diffuse parenchyma and fibres with bordered pits, which are usually associated with an unspecialized structure."

The Zygophyllaceae have many economic uses; Hutchinson (1967, pp. 612, 613) gives a good summary of these (see also *Guaiacum* below). *Kallstroemia hirsutissima* Vail in Small and *Peganum Harmala* are reported (cf. Kingsbury, 1964) to poison cattle, and *Tribulus terrestris* (see below) to poison sheep. Alkaloids have been reported to occur in many genera, and it is these that are suspected in stock poisoning by the species noted above and others in the Old World.

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#### KEY TO THE GENERA OF ZYGOPHYLLACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: Nodes angled or swollen; leaves opposite, even-pinnately compound, stipulate; flowers terminal or pseudaxillary, 5-merous, hypogynous, perfect, with an extrastaminal and/or intrastaminal disc.



- A. Plants herbaceous; flowers yellow; stamens unappendaged; fruit a schizocarp separating at maturity into 5 or 10 mericarps.
  - B. Fruit tuberculate, at maturity separating into 10 mericarps, beak persistent on receptacle; intrastaminal glands absent. . . . 1. *Kallstroemia*.
  - B. Fruit spiny, at maturity separating into 5 mericarps, beak falling with mericarps; intrastaminal glands present. . . . . 2. *Tribulus*.
- A. Plants woody (trees or shrubs); flowers blue or purple; stamens appendaged; fruit a 5-lobed septicidal capsule. . . . . 3. *Guaiaecum*.

Subfam. TRIBULOIDEAE Porter

1. ***Kallstroemia*** Scopoli, Introd. Hist. Nat. 212. 1777.

Annual [occasionally perennial] herbs; stems herbaceous [to suffrutescent], diffusely branched, prostrate to decumbent or ascending, terete, somewhat succulent, becoming striate on drying, densely pubescent to glabrate, spreading radially from a central tap root to 1 m. or more long. Leaves opposite, elliptic to broadly obovate, abruptly even-pinnate, one of each pair alternately smaller or sometimes abortive; leaflets (2) 3–5 (6) [–10] pairs, opposite, entire, subsessile, elliptic to broadly oblong or obovate, somewhat unequal in size, those on one side of rachis slightly smaller, lowest pair markedly unequal, terminal pair directed forward and more falcate, pubescent to glabrate; stipules foliaceous. Flowers solitary, pseudaxillary, regular; peduncles emerging from axils of alternately smaller leaves. Sepals 5 [6], free, pubescent, persistent [rarely caducous]. Petals 5 [6], white to orange, the same basally or green to brighter than apex, free, spreading (the corolla cuplike), fugacious, [usually] marcescent, convolute. Disc fleshy, annular, obscurely 10[–12]-lobed. Stamens 10 [12], the 5 [6] exterior ones opposite petals, somewhat longer and adnate basally to petals, the 5 [6] opposite sepals subtended abaxially by a small bilobed gland; filaments filiform or subulate [rarely basally winged], unappendaged, inserted on disc; anthers globose or ovoid [to linear-oblong] or rarely linear, those opposite sepals rarely aborting. Style simple, cylindrical to [broadly] conical, more or less 10[–12]-ridged, persisting to form a beak on fruit; stigma capitate or oblong [or clavate], 10[–12]-ridged or -lobed, papillose [rarely coarsely canescent], terminal [rarely extending down almost to base of style]; ovary sessile, 10[–12]-lobed and -loculate, ovoid or pyramidal [globose or occasionally conical], glabrous to pubescent; ovules 1 per locule, pendulous, placentation axile, sometimes 1 or more aborting. Fruit 10[–12]-lobed, ovoid [occasionally conical or rarely pyramidal], glabrous or pubescent, at maturity dividing septicidally and separating from a persistent styliiferous axis into 10[–12] or occasionally fewer mericarps; mericarps 1-loculate, 1-seeded, obliquely triangular, wedge shaped, more or less tuberculate or rugose abaxially. Seeds oblong-ovoid, obliquely pendulous; seed coat membranaceous; embryo straight; endosperm absent; germination epigeal. TYPE SPECIES: *Kallstroemia maxima* (L.) Hooker & Arn. (*Tribulus maximus* L.). (Origin of name unknown, although it has been suggested that it is derived from that of Anders Kallström, a contemporary of Scopoli.)



The largest New World genus of the family, with 17 species (see Porter, 1969a), these ranging from Illinois to Argentina, in open, disturbed habitats. Even in the tropics, *Kallstroemia* species invariably will be found in the driest localities of a particular area. Nine species are basically of a southwestern United States-northern Mexican distribution, and the least specialized species of the genus, *K. perennans* Turner, occurs in the Big Bend region of Texas. Three species are basically Caribbean in distribution, and five are South American. Three species occur in our area.

The most common *Kallstroemia* in the Southeast is *K. maxima*. This primarily Caribbean species occurs from Colombia and Venezuela north to Sinaloa, Mexico, on the west, and to South Carolina, on the east, with a waif found as far north as Pennsylvania (Porter, 1970). In our area it has been collected on sandy, disturbed soils near the sea in Florida, Georgia, and South Carolina. It is easily distinguished by its glabrous fruits.

*Kallstroemia parviflora* Norton has been collected once in Oktibbeha County, Mississippi, where it apparently did not form a persistent colony. It has also been found as a waif in Maryland (Porter, 1970). It is indigenous to grassy, disturbed areas from Illinois, west to Arizona, and south to central Mexico, and it is an introduced weed in Peru. The strigose to glabrous beak on the fruit is two to three times as long as the ovoid, strigose body.

*Kallstroemia pubescens* (G. Don) Dandy in Keay,  $2n = 32$ , is known in the United States only from Apalachicola, Florida, where it may or may not have persisted. This basically Caribbean species, known from Peru northward to Sinaloa, Mexico, and the Antilles, was first described from what is now Ghana. It has also been collected in the Ivory Coast and in India (Bennett, 1965). In the Greater Antilles it is known only from Jamaica (Proctor, 1967) and Puerto Rico. The short-pilose to glabrous beak on the fruit is as long as the pyramidal, densely appressed short-pilose body.

Four species grown in the greenhouse have been found to be self-compatible (Porter, 1969a), a decided advantage for weedy plants. They (and apparently all others, except *Kallstroemia perennans*) also can be self-pollinated by an upward and inward movement of the stamens and petals as the flower, which is open in the morning, closes in early afternoon.

Little is known of natural relationships within the genus. The only chromosome number known is that of *Kallstroemia pubescens* (Datta, 1968). Hybridization between *K. maxima* and *K. pubescens*, in Colombia, and between *K. maxima* and *K. Rosei* Rydb. in Vail & Rydb., in Mexico, is suspected (Porter, 1969a).

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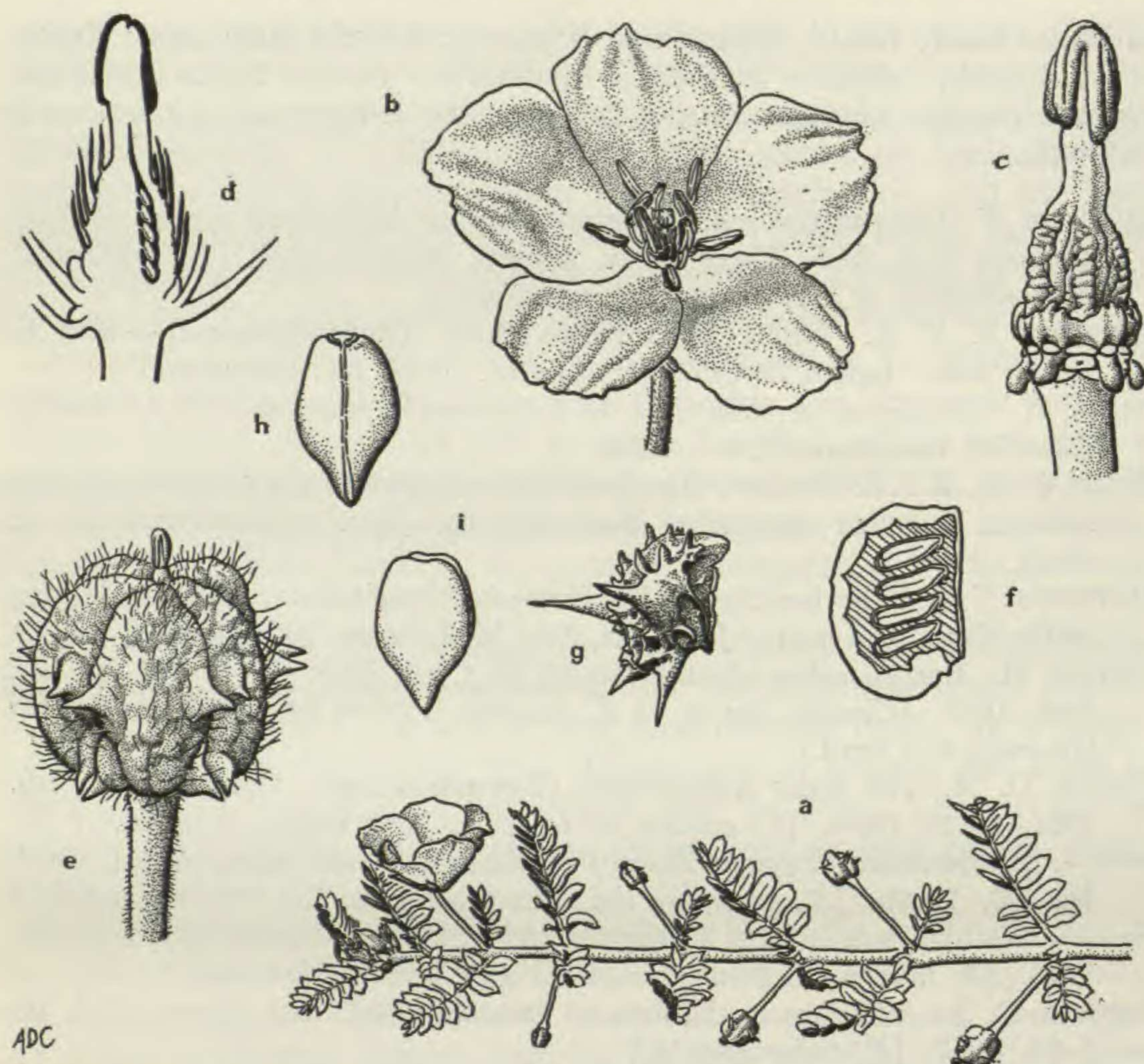
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## 2. *Tribulus* Linnaeus, Sp. Pl. 1: 386. 1753; Gen. Pl. ed. 5. 183. 1754.

Annual or occasionally perennial herbs [very rarely shrubby]; stems herbaceous to suffrutescent, diffusely branched, prostrate to decumbent or ascending, terete, somewhat succulent, becoming striate on drying, densely pubescent to glabrate, spreading radially from a central tap root to 1[–3] m. long. Leaves opposite, elliptical in outline, abruptly even-pinnate, one of each pair alternately smaller or sometimes aborting; leaflets 3–7[–10] pairs, opposite, entire, sessile to very shortly petiolulate, oblong to ovate or elliptical, terminal pair pointed forward, pubescent; stipules foliaceous. Flowers solitary, pseudaxillary, regular; peduncles emerging from axils of alternately smaller leaves. Sepals 5, free, pubescent, caducous. Petals 5, bright yellow or rarely white, darker basally, free, spreading (the corolla cuplike), deciduous, imbricate. Disc fleshy, 10-lobed, annular. Stamens 10, the outer whorl of 5 opposite petals, somewhat longer, and adnate





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FIGURE 1. *Tribulus*. a-h, *T. cistoides*: a, tip of prostrate branch with flower and developing fruits,  $\times 1/2$ ; b, flower,  $\times 1\ 1/2$ ; c, gynoecium and staminal glands, the intrastaminal ones united around base of ovary, the extrastaminal ones subtending stamens opposite sepals, the positions of stamens, petals, and sepals unshaded, hairs on ovary not shown,  $\times 6$ ; d, flower in semidiagrammatic vertical section to show placentation and positions of stamens, glands, sepals, and petals — base of sepal and stamen opposite it to left, base of petal and stamen opposite it to right,  $\times 6$ ; e, nearly mature but still green fruit,  $\times 2$ ; f, one mericarp of fruit in median vertical section showing four seeds and embryos,  $\times 2$ ; g, stony part of mature mericarp, softer outer tissues removed,  $\times 2$ ; h, seed,  $\times 6$ ; i, embryo,  $\times 6$ .

basally to petals, the inner 5 opposite sepals and subtended both ad- and abaxially by nectariferous glands, the intrastaminal glands free or connate to form an urceolate ring surrounding ovary base; filaments filiform or subulate, unappendaged, inserted on disc; anthers cordate to sagittate. Style simple, stout, cylindrical, 5-ridged, deciduous; stigma terminal, pyramidal or globose to inequilateral, 5-lobed, papillose; ovary sessile, 5-lobed and -loculate, ovoid or globose, densely pubescent; ovules 3-5 per locule, pendulous, superposed in 2 vertical rows on placenta, placentation axile. Fruit 5-angled, usually horizontally depressed, pubescent, at maturity dividing septicidally and separating into 5 or rarely fewer mericarps



and leaving no central axis; mericarps broadly triangular, each divided internally by oblique transverse septa into 2–5 one-seeded compartments, spiny [or winged or rarely only tuberculate abaxially]. Seeds oblong-ovoid, obliquely pendulous, horizontally arranged one above the other; seed coat membranaceous; embryo straight; endosperm absent; germination hypogeal. LECTOTYPE SPECIES: *Tribulus terrestris* L.; see Vail & Rydberg, N. Am. Fl. 25: 109. 1910. (Name from Greek *tribolos*, a kind of caltrop, an iron instrument with four spines arranged so that one always projects upward, used to impede cavalry.) — PUNCTURE WEED, CALTROP, BURR-NUT.

An Old World genus of several dozen species, commonest in Africa and the Near East. Most are weedy occupants of dry, disturbed habitats, either natural or man induced. The spiny mericarps of many species provide an ideal mechanism for dissemination, and man has long been involved in their spread. Three species (two represented in our area) have been introduced into the New World.

*Tribulus cistoides* L., burr-nut,  $2n = 12$ , is common in southern Florida, and it is also known from northwestern Florida, Georgia, and Louisiana. Native to tropical and subtropical southern Africa, it is now a weed throughout the drier tropics, mainly in maritime habitats. It is an attractive plant with showy yellow flowers two to four centimeters in diameter that have led to the common name "Jamaica buttercup." The plant is occasionally grown in sandy soils as a garden ornamental or along roads to stabilize shifting soils.

*Tribulus terrestris* L., puncture vine, is a noxious roadside weed most common in the West and Midwest. In our area it has been collected sporadically in Florida, Louisiana, South Carolina, and Tennessee, and more commonly in Arkansas. It is native to the Mediterranean region, probably to northern Africa. A widespread weed in the warm-temperate areas of the world, it occurs on all continents but Antarctica but has been found only rarely in the tropics. The flowers are one centimeter or less in diameter.

*Tribulus cistoides* and *T. terrestris* are easily distinguished in the southeastern United States by flower size. In some other areas, however, the flower size of one species may approach or overlap the other, and the morphology of the intrastaminal glands must be relied upon. They are five, triangular, and free in *T. terrestris*, and connate into a five-lobed urceolate ring in *T. cistoides*. A breakdown in the species-specificity of this character in the equatorial Galápagos Islands has led to the hypothesis that hybridization between these two introduced species has taken place there (Porter, 1971a & b).

After trying unsuccessfully for some 50 years to control *Tribulus terrestris* by chemical means, the California Department of Agriculture in 1961 imported two species of weevil from India for biological control. The larvae of both feed selectively on *T. terrestris*, *Microlarinus lareynii* (Jacquelin du Val) on the seeds and *M. lypriformis* (Wollaston) on the



stems. These weevils appear to be well on the way to controlling *T. terrestris* in the Southwest.

In Africa, Australia, and the United States ingestion of the plant by sheep leads to "geeldikkop" or "bighead," a fatal disease involving hepatogenic photosensitization. Both nitrate and selenium poisoning may be involved (see Kingsbury, above).

Diploid ( $2n = 12$ ), tetraploid ( $2n = 24$ ), hexaploid ( $2n = 36$ ), and octoploid ( $2n = 48$ ) races have been reported for *Tribulus terrestris*, but only diploids have been found in *T. cistoides*. According to Malik (1966) the races of *T. terrestris* can be distinguished by pollen and flower size. Chromosome numbers are not known for any other species of this taxonomically difficult and poorly-known genus.

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#### Subfam. ZYGOPHYLLOIDEAE

3. **Guaiacum** Linnaeus, Sp. Pl. 1: 381. 1753, 'Guajacum'; Gen. Pl. ed. 5. 179. 1754.

Evergreen [deciduous] trees [or shrubs], [1–]2.5–10[–20] m. high, with a dense rounded crown; trunk short, stout, occasionally 1[–2] m. in diameter, the bark thin, light gray [light brown or olive-green], fissured vertically [smooth], separating on the surface into thin whitish [olive-green] scales, the wood hard and resinous, the heartwood dark green or yellow-brown, the sapwood thin and yellow; branches stout, slightly angled, pubescent, becoming glabrate, spreading, the branchlets stout, slightly angled, with conspicuously swollen nodes, green, becoming light gray, fissured, pubescent, becoming glabrate. Leaves opposite [sometimes crowded on short lateral branchlets], even-pinnate, the petiole and rachis pubescent [glabrous]; leaflets [1–]3–5[–7] pairs, opposite, entire, sessile, [narrowly] elliptic to obliquely oblong or obovate [ovate], rounded [acute to obtuse or retuse] and mucronate apically, inequilateral basally, [membranaceous to] subcoriaceous or coriaceous, pubescent to glabrate, somewhat unequal in size, basal [apical] pair largest; stipules acuminate, usually mucronulate, usually deciduous, sometimes persistent. Flowers showy, solitary to several [or many], slightly irregular by twisting of petals; peduncles borne in axils of minute axillary bracts between stipules [sometimes crowded on short lateral branchlets], shorter than leaves. Sepals 4 or 5, free to slightly connate basally, obovate, pubescent, smaller than petals, deciduous. Petals 4 or 5, blue [violet or rarely white] drying yellow, free, obovate, rounded to lobed apically, clawed and twisted basally, spreading, glabrous or pubescent, imbricate. Disc annular, inconspicuous.



Stamens 8–10, free; filaments subulate or slightly winged basally, unappendaged, inserted on disc; anthers versatile, sagittate or cordate. Style simple, slender, subulate, persisting and forming a beak on fruit; stigma minute, entire or with as many lobes as ovary; ovary on a short gynophore, [2–] 4- or 5-lobed and -loculate, obovoid [obcordate and flattened], glabrous [pubescent]; ovules 8–10 per locule, pendulous, the placentation axile. Fruit a capsule, [2–] 4- or 5-lobed and -winged, obovoid [obcordate and flattened], broadest apically, smooth, glabrous [pubescent], coriaceous, [green] orange to yellowish[-brown], narrowed basally into a short gynophore, septicidally dehiscent. Seeds ovoid, 1 per locule, [1 or 2] 4 or 5 maturing per fruit, surrounded by a thick fleshy red aril; seed coat membranaceous, brown or black; embryo straight, cotyledons foliaceous; endosperm present. LECTOTYPE SPECIES: *G. officinale* L.; see Vail & Rydberg, N. Am. Fl. 25: 105. 1910. (Name from guayacán, a Caribbean Indian name for species of *Guaiaecum* and *Tabebuia* Gomes ex DC. [Bignoniaceae] with extremely hard wood.) — LIGNUM VITAE.

A New World genus of four or five species occurring from Sonora, Mexico, south to Costa Rica and throughout the Caribbean basin north to the Florida Keys and the Bahamas. *Guaiaecum sanctum* L., a low gnarled tree rarely up to 10 m. tall, reaches our area on the Florida Keys, where it was formerly of rather common occurrence. With the destruction of the tropical hardwood forests there, the only remaining trees of any size appear to be on Lignumvitae Key. It also occurs in the Bahamas, Cuba, Hispaniola, Puerto Rico, Yucatán, Guatemala, Honduras, Nicaragua, and Costa Rica. The related but quite distinct *G. officinale* L.,  $2n = ca. 26$ , is indigenous from the Bahamas and Greater Antilles, south through the Lesser Antilles to Tobago, and in Guyana, Venezuela, and Colombia. *Guaiaecum Coulteri* Gray occurs from northwestern Mexico to Central America, and the closely related *G. unijugum* T. S. Brandegees is endemic to the southern tip of Baja California. Both *G. sanctum* and *G. officinale* are cultivated in southern Florida (and elsewhere in tropical America) for their handsome blue flowers, colorful orange or yellow fruits, and attractive dark green persistent foliage. The violet-flowered *G. Coulteri* is grown to a much lesser extent.

The leaves of *Guaiaecum sanctum* have three or four pairs of leaflets, the lowermost and middle pairs being largest, and the fruits are pointed at the apex, are four- or five-lobed and -winged, and have four or five seeds. The leaves of *G. officinale* have two or three pairs of obovate leaflets, with the terminal pair the largest, and the fruits are emarginate or heart shaped at the apex and are two-lobed and -winged with one or two seeds. Both are evergreen plants with flowers 2.5 cm. or less in diameter that are produced as the new foliage is expanding. *Guaiaecum Coulteri* has leaves with three to seven pairs of narrowly elliptic leaflets, the middle pairs being largest, and pointed four- or five-lobed and -winged fruits with four or five seeds. The flowers are larger than 2.5 cm. in diameter, and the petals are more dis-



tinctly clawed than in the two preceding species. Flowering usually begins while the plant is leafless before the new leaves unfold.

*Guaiaacum sanctum* and *G. officinale* are sympatric in the Greater Antilles, and *G. sanctum* and *G. Coulteri* are sympatric in Central America. The name *G. guatemalense* Planchon ex Rydb. has been applied to collections from Guatemala, Honduras, Nicaragua, and Costa Rica. However, the range in variation exhibited by these specimens, plus the observation that some have much-reduced seed-set, suggests that *G. Coulteri* and *G. sanctum* are hybridizing and introgressing in Central America.

*Guaiaacum* is closely related to *Porlieria* Ruiz & Pavon, which has about four species, one in Texas and northeastern Mexico and several in southern South America. *Porlieria* differs from *Guaiaacum* in having persistent, commonly spinescent stipules; more, smaller, and narrower leaflets; staminal appendages; and two to four ovules per locule. Further study may prove them to be congeneric.

The wood and resin of *Guaiaacum* species, especially of *G. officinale* and *G. sanctum*, have long been the most important economic products of the family. Soon after Columbus' voyage to the New World, large quantities of wood were being shipped to Europe because of the supposed medicinal value of an extract of the heartwood. Sold by the pound, the wood was quite expensive, considering that its specific gravity is about 1.2. So many trees and populations have been destroyed that these plants have become extinct or very rare on many of the Caribbean islands. They are very slow growing and are not quick to recolonize areas from which they have been removed.

The name *lignum vitae* (wood of life) derives from the belief that the wood exhibited miraculous medicinal properties. For over 200 years it was considered a specific remedy for venereal disease. With the invention of steam-powered ships, the wood became important for bearings or bushing blocks to line the stern tubes of propeller shafts. The wood is one of the strongest known, and its high resin content and concomitant self-lubricating properties, combined with its strength, make it ideal for uses under conditions of stress and sea water. Today the wood is used mainly for the manufacture of such turned objects as mallets, pulley sheaves, caster wheels, bowling balls, stencil and chisel blocks, mortars and pestles, brush backs, planes, and the like. For good discussions of the sources of supply, marketing, and uses of *lignum vitae*, see Record (1921) and Longwood (1962).

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